INHERITANCE IN POTATOES

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A STUDY of the behavior of certain plant characters in inheritance formed part of an investigation into the factors connected with the improvement of the common potato as a commercial crop, begun at the Connecticut Agricultural Experiment Station in 1906. This work was really a continuation of investigations made by the writer at the University of Illinois from 1902 to 1905, along broader and somewhat different lines. In 1908[1] the many disheartening difficulties attending hybridization were discussed, but it was shown to be possible to overcome several of the obstacles by proper treatment. The conclusions drawn at that time have not been changed by further experience, but the hindrances caused by external conditions not under control have been so great that the work has been discontinued. For example, in 1908 a prolonged drought at the time the fruits were forming, caused one hundred and fifty cross- and self-pollinated seed-berries to drop off while yet too immature for the seed to germinate. Not a single hand-pollinated flower matured its fruit.

Recently, a part of the pedigree records were lost in a fire which destroyed one of the buildings of the Connecticut Agricultural Experiment Station. For these reasons the data reported here do not represent fairly the amount of work done upon the subject, for the actual number of plants under observation was considerably larger than the figures reported. The complete figures had been studied with some care before the loss of the records, and it is thought that the remaining records are a fair sample of the whole.

The records contain observations on only one genera-

[1] Some essential points in potato breeding. Biennial Report, Conn. Agr. Exp. Station, 1907–1908, 429–447, 1908.

tion of plants, together with the characters possessed by their parents. I have endeavored to find what characters were possessed by the parents of the varieties used in crossing but have found no trustworthy data. The following conclusions, therefore, are tentative. Nothing is known about the behavior of the characters when extracted. The data show that *certain characters segregate,* they give some evidence as to dominance and recessiveness, but they do not show the exact behavior of the Mendelian factors concerned, under different combinations.

Color in the Plant Stem

Many varieties have a purple anthocyan sap color which gives the plant stem a dark appearance quite distinct from the clear green stems of the varieties in which it is absent. The color is variable in amount in different varieties. In some it extends throughout the petioles and petiolules; in others it can only be detected on the stems of the young seedling. My counts were made on seedlings about four inches high.

The color is evidently of the same nature as that found in many other cultivated plants. Its widespread occurrence and seeming uselessness in the plant's economy would place it in the category of typical varietal characters in the sense used by De Vries. It forms a single allelomorphic pair with its absence.

One purple-stemmed variety selfed gave all purple-stemmed progeny. Four purple varieties selfed, each showed segregation into two distinct classes, purple and non-purple. Fifty-four purple plants and seventeen non-purple plants were obtained. (These figures as well as those that follow are the records saved from the fire.) In each of these cases we may take it that the parent plants were heterozygous for the purple color, and approximated the simple three to one Mendelian ratio when self-pollinated. Four green-stemmed varieties were also selfed, and produced nothing but green-stemmed progeny.

One of these pure green-stemmed varieties was crossed on one of the heterozygous purples, and thirteen seedlings were obtained. Six plants were purple-stemmed and seven were green-stemmed. This result is what would be expected when crossing DR $\times$ R.

COLOR IN THE FLOWERS

All potato flowers have a ray of yellow extending from the limb of the corolla toward the apex of each lobe. The remainder of the corolla is either white or purple. There is wide zygotic (in potatoes, therefore, varietal) variation in the intensity of the purple sap color, but the flowers should probably be classed as either purple or white. The fact that the variety color, whether light or dark, remains true when propagated asexually, does not necessitate more than one Mendelian pair. It is undoubtedly a quantitative difference in the same pigment which is kept constant by the asexual method. Why somatic cell divisions should reproduce a color shade so exactly, while sexual reproduction gives rise to varying shades is unknown. It is the more peculiar since in animals visible division of the chromatin appears to be much more accurate in the sexual cells than in the somatic cells. The somatic cell appears to have the power of developing and of regenerating only the quantity of color originally apportioned to it, except on the rare occasions when all of the potential color activity goes to one daughter cell and the other is left without it. When this occurs, branches resulting from the descendants of the second cell are "sports" or "bud-variations" in which the original character is lost.

Only two varieties of potatoes with flowers other than purple or white have been noticed. The variety *Holland fleur de June* has blossoms which are decidedly yellow. Several attempts to self this variety and to cross it with other varieties failed. One other variety, a nameless seedling of unknown origin, possessed a true blue flower. No admixture of red which would give it a

purple tinge could be detected. Even this color, however, may be of the same nature as the purple color, the difference being in the completeness of the reaction forming the blue dye. It will be remembered that litmus reacts in this manner. Several cross-pollinated and several self-pollinated fruits were obtained from this variety, but none of the seedlings had flowered in 1909, the second year of their growth.

The seedlings of the potato are very slow to flower in a New England environment, and but few flower records were obtained among several hundred plants. One selfed variety with purple flowers gave progeny all with colored flowers. Three selfed varieties with purple flowers gave both purple and white flowers: the total number of seedlings that flowered was nineteen, of which fourteen were purple-flowered and five were white-flowered. Three selfed white-flowered varieties gave nothing but white-flowered progeny.

Since three white-flowered varieties gave nothing but white flowers and three out of four colored varieties showed a hybrid condition with segregation of color, the purple is probably dominant to its absence. Color and no color is probably a single Mendelian pair, but this can not be stated with certainty from such meager data.

Color in the Tubers

Potato tubers, when colored,[2] are either purple or red. In both cases the color may extend over the entire tuber or may be limited in extent. No definite mosaic pattern is formed when the color is limited, but the splashes of color are restricted to pretty definite areas. It is probably due to a separate Mendelian factor, for the mosaic varieties and the self-colored varieties are distinct. Tuber color varies quantitatively more than flower color. Many varieties show no color in the skin, and can be classified only by examining the young shoots when the

[2] Colorless skins may vary from white to dark brown in different varieties. This is entirely due to their possessing corky layers of various thicknesses.

latter are about half an inch in length. The progeny of such varieties belong to the same classes as the progeny of self-colored varieties. They give fewer self-colored seedlings, however, which may be due to the action of one or more unknown heritable factors. I have not attempted to separate the self-colored from those showing color in the young shoots, but have classified both as colored varieties.

The results of selfing varieties with different color characters are as follows:

Selfed purples gave either all purples (one variety); purples, reds and colorless (two varieties); or purples and colorless (three varieties). Selfed reds gave either all reds (two varieties), or reds and colorless (two varieties). Selfed red varieties gave no purple progeny. Three colorless varieties (that is, no color in *either* the *tuber skin* or *young shoots*) were selfed, giving all colorless progeny.

Without considering factors for limiting color, these results seem to show that purple and red are separate Mendelian units, each dominant to its absence, and that purple is epistatic to red.

It is an interesting fact that although the purple varieties and the red varieties are distinct color types without intermediates and that mosaic varieties of each are known, yet in no case has a mosaic variety appeared in which splashes of the two colors are found. We may conclude therefore that the two colors are formed by the action of other factors upon the same chemical constituent. If we assume that the red color is a lower form of oxidation than the purple color and that they are produced by different oxidases R and P acting upon the same substance C, the results obtained are explained, for the presence of P would oxidize all of the stubstrate to the purple color.

SHAPE OF TUBER

Potato tubers vary in shape from a length six times the median diameter to a length about the same as the

median diameter. The varieties, the length of whose tubers is not over one and one-quarter times the medium diameter, I have called round. Two selfed round varieties gave only round progeny. Twelve varieties with oval tubers when selfed gave elongated, oval and round progeny. The ratio of other types to round was about nine to one. Either there is a series of factors for shape with the round type as the final subtraction form, or the oval types are heterozygotes of elongated and round. The latter interpretation is more likely to be correct, because oval types have been the popular market types for many years and therefore been used as parents in crosses.

Depth of Eyes

Shallow buds or eyes are required for profitable commercial varieties, yet from one fifteenth to one fourth of the progeny of ten selfed varieties were deep-eyed forms. Three selfed varieties gave no deep-eyed progeny. No progeny of deep-eyed seedlings were obtained, but it seems probable that this character is recessive to shallow eye.

The writer is fully aware that these few observations do not prove that the characters in which potato varieties differ all segregate in Mendelian proportions after crossing. A long series of crosses is necessary to analyze correctly the behavior in inheritance of such characters as shape. On the other hand, the color characters in stem, blossom and tuber are definite and discontinuous, and are alternative in inheritance. The chaotic appearance of the progeny of our commercial potatoes is only apparent. They readily fall into a simple classification and their exact behavior in inheritance could be readily determined if it were not for the difficulties attending successful crossing.

As the writer has previously stated,[3] certain characters pair with their own absence in crossing and these

[3] "The Transmission of Variations in the Potato in Asexual Reproduction," Biennial Report, Conn Agr. Exp. Sta. 1909–1910, 119–161, 1910.

character pairs are the ones affected when a somatic mutation or bud variation occurs in asexual reproduction. Simple loss of the factor takes place. Segregation, therefore, takes place at other times than the reduction of the chromosomes.

In a previous paper,[4] the writer analyzed the data then extant concerning the hypothesis of degeneration or "running out" of potato varieties. The conclusion was that no degeneration due to continued asexual propagation occurs. No data have been obtained which refute this view, but the study of progeny of selfed potato varieties has suggested an explanation of a certain amount of diminution in yield after long-continued asexual propagation. All commercial potato varieties which have been selfed and their progeny grown, have proved to be heterozygous in at least two characters. It has been shown[5] that when maize biotypes are crossed, the F_1 generation has greater vigor and gives larger yields than the parents. It is a condition apart from inheritance, and is probably due to the heterozygous condition of certain characters in the germ cells. It may be correlated with the actual mechanical operation of segregation. Since potato varieties are retained in cultivation on the basis of yield and since those on the market have been found to be heterozygous in many of their characters, probably the same phenomenon is the cause. May there not be a gradual loss of the stimulus due to crossing through continued bud propagation, so that the variety has only the vigor of one homozygous in the same characters? The variety of course remains heterozygous for those characters in which it was originally heterozygous, yet there may be a gradual decline of the stimulus to cell division than it once possessed.

[4] A "Study of the Factors influencing the Improvement of the Potato," Bull. Ill. Agr. Exp. Sta., No. 127, 375–456, 1908.

[5] East, E. M., "The Distinction between Development and Heredity in Inbreeding," AMER. NAT., 43: 173–181, 1909.